A NEW SPECIES OF PALORCHESTIDAE (MARSUPIALIA) FROM THE LATE MIDDLE TO EARLY LATE MIOCENE ENCORE LOCAL FAUNA, RIVERSLEIGH, NORTHWESTERN QUEENSLAND

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A single palorchestid M^1 from the Encore Local Fauna, Riversleigh, northwestern Queensland is described as *Palorchestes anulus* sp. nov. In size and morphology, it is intermediate between the M^1 of middle Miocene *Propalorchestes novaculacephalus* from System C deposits, Riversleigh and the Bullock Creek Local Fauna, Northern Territory, and that of *Palorchestes painei* from the late Miocene Alcoota Local Fauna, Northern Territory. These relationships support an early late Miocene age for the Encore Local Fauna and confirm that *Propalorchestes* is the sister-group of *Palorchestes*. Consequently, the monophyly of Palorchestidae is cast further in doubt. Species of *Ngapakaldia* and *Pitikantia* may be more appropriately regarded as plesiomorphic members of Diprotodontidae.
Palorchestidae, Palorchestes, Propalorchestes, late Miocene, Riversleigh.

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A recently discovered upper molar from Encore Site on the Gag Plateau, Riversleigh has increased the late Oligocene to late middle Miocene material of Palorchestinae to 9 specimens. This paucity of material, which prior to 1986 consisted exclusively of the highly derived *Palorchestes*, has made resolution of relationships within the family difficult. Although *Palorchestes anulus* sp. nov. is only known from an isolated M^1, it adds substantially to phylogenetic understanding within the family.

On the basis of vertebrate stage-of-evolution biocorrelation the Encore Local Fauna is currently regarded as late middle to early late Miocene (approximately 10Ma; Archer et al., 1995). Taxa from Encore Site are more derived than those characteristic of Riversleigh's upper System C assemblages yet plesiomorphic relative to related taxa of the late Miocene Alcoota Local Fauna, Northern Territory (Archer et al., 1995). The species described below supports an early late Miocene age.

Institutional abbreviations used here are as follows: QMF, Queensland Museum palaeontological collection; CPC, Commonwealth Palaeontological Collection at the Australian Geological Survey Organisation, Canberra; NTMP, Art Gallery and Museum of the Northern Territory palaeontological collection; SAMP, South Australian Museum; UCMP, University of California, Berkeley. Cusp nomenclature follows Archer (1984) and Rich et al. (1978) except that their hypocone of upper molars is the metaconule following Tedford & Woodburne (1987). Molar number homology follows Luckett (1993). Higher level systematic nomenclature follows Aplin & Archer (1987).

SYSTEMATIC PALAEONTOLOGY

Order DIPROTODONTIA Owen, 1866
Suborder VOMBATIFORMES Woodburne, 1984
Infraorder VOMBATOMORPHIA Aplin & Archer, 1987
Superfamily DIPROTODONTOIDEA Archer & Bartholomai, 1978
Family PALORCHESTIDAE Tate, 1948 emend. Archer & Bartholomai, 1978

Palorchestes Owen, 1873

TYPE SPECIES. *Palorchestes azael* Owen, 1873.
OTHER SPECIES. *P. parvus* De Vis, 1895; *P. painei* Woodburne, 1967; *P. selestiae* Mackness, 1995.

Palorchestes anulus sp. nov.
(Figs 1-2, Table 1)

MATERIAL. Holotype, QMF30792, a right M^1 missing the posterior cingulum and anterior and posterior roots from the late middle Miocene to early late Miocene Encore Local Fauna, on the Gag Plateau, Riversleigh.

ETYMOLOGY. Latin *anulus*, link; refers to its being a structural link between *Propalorchestes* and *Pal-*

TABLE 1. Measurements (mm) of palorchestid M^1.

Species	No	Length	Anterior width	Posterior width
Palorchestes anulus	QMF30792	17.1	13.5	13.0
Pr. ponticulus	NTM P895-1	14.3	11.5	10.9
	QMF30883	15.3	-	-
	QMF30884	16.2	12.6	11.0
	QMF20612	15.2	-	10.8
Pr. novo-culacephalus	NTMP862-27	16.8	13.2	12.0
P. selestiae	QMF12455	22.6	16.6	16.9
P. painei	UCMP 70553 R	16.5	13.6	13.8
	UCMP 70553 L	16.8	14.4	13.7
	UCMP 70550	16.7	13.9	13.7
	UCMP 66521	17.8	14.0	13.2
	CPC6752	18.2	14.3	-
P. parvus	QMF 784	20.7	15.7	15.4
	QMF12476	-	15.4	15.3
	QMF2963	19.3	14.9	14.4
	QMF3719	19.3	15.0	14.2
	QMF2967	19.4	15.6	15.6
	QMF2965	20.9	-	14.5
P. azael	QMF772	26.6	21.9	21.5
	QMF3837	25.8	20.7	19.7
	P31370	28.3	21.8	21.4
	P31371	28.3	22.6	21.9
	P31372	26.1	22.9	21.9

orchestes and to the distinct midlink, a character of *Palorchestes*.

COMPARISON. *Palorchestes anulus* differs from *P. painei* in being proportionately narrower anteriorly and posteriorly, in its poorly developed lingual cingulum, more open transverse median valley lingually, less tightly V-shaped transverse median valley in lingual view and less well-developed hindlink.

Palorchestes anulus differs from *P. parvus*, *P. selestiae* and *P. azael* in being smaller; in having generally less well-developed links; in having a shallower, more open transverse median valley; in having a more buccally positioned midlink; in having a less well-developed, lower, less buccally extensive (i.e. in lacking the anterobuccal cingulum) anterior cingulum (compared with the high, loph-like anterior cingulum in both *P. parvus* and *P. azael*) and consequently, in lacking the deep valleys formed between the anterior cingulum and the anterior base of the protoloph.

Palorchestes anulus differs from both *P. parvus* and *P. azael*: in lacking the second medial forelink; in having a less well-developed midlink which is deeply V-shaped, its respective anterior and posterior crests meeting lower in the transverse median valley (and more buccally) than the well-developed structure in both *P. parvus* and *P. azael*; in lacking the second buccal midlink, and having only a poorly-developed accessory crest extending anteriorly from a medial point on the metaloph; in having a poorly-developed lingual cingulum; in lacking a buccal cingulum; and in having well-developed postparaconal and postmetaconal crests extending posteriorly from the apices of the paracone and metacone respectively.

Palorchestes anulus differs from *P. selestiae*: in having a short crescentic lingual cingulum; in lacking the anterolingual forelink; in lacking the secondary midlink and the minor lingual midlink; and in having less-crenulated enamel at the base of the protoloph and metaloph.

Palorchestes anulus differs from *P. parvus* in having a straighter, less crescentic metaloph and in having a less crenulate transverse median valley.

Palorchestes anulus differs from *P. azael* in lacking the well- developed lingual midlink; in having a better-developed posterior cingulum; and in having a hindlink developed.

DESCRIPTION. Tooth rectangular, bilophodont, consisting of an anterior protoloph connecting the protocone with the paracone, and a posterior metaloph connecting the metacone with the metaconule. Protoloph anteriorly convex; metaloph slightly more linear, with its lingual end deflected posteriorly. Metaconule highest cusp; the paracone and protocone subequal in height; metacone lowest cusp (taking into account slight wear on the apices of the major cusps). Anterior cingulum well-defined but low on the anterior base of the crown, extending lingually from the anterobuccal tooth margin to the anterolingual base of the protocone. Lingual cingulum short, poorly defined, connecting the posterolingual base of the protocone to the anterolingual base of the metaconule. Posterior cingulum not preserved (but suggested by the short crest at the posterolingual base of the metaconule).

Forelink well-developed, extending anteriorly

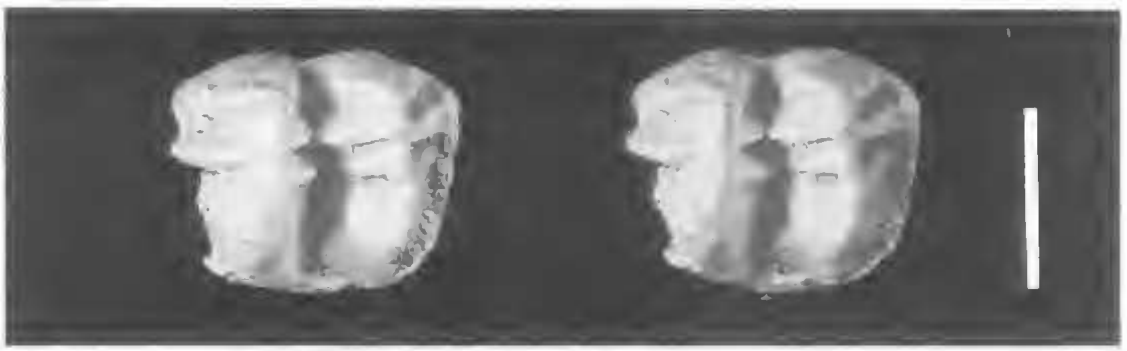

FIG. 1 *Palorchestes anulus* sp. nov. Holotype, QMF30792: Occlusal stereopair of right M^1. Bar indicates 10mm.

from the apex of the protoloph at a point slightly lingual to the paracone apex, meeting the anterior cingulum at the parastylar corner of tooth. Two accessory crests (or incipient links) poorly-defined: one originating at the paracone and fading down the anterobuccal face of the crown; the second originating from the protoloph at a point slightly lingual to the main forelink, extending anteriorly and slightly buccally, along the longitudinal axis of the tooth, terminating in the valley between the anterior base of the protoloph and the anterior cingulum. Single midlink formed by the junction of respective anterior and posterior crests from the metaloph and protoloph meeting low in the transverse median valley (making the link sharply V-shaped in lateral view) approximately 4mm from the buccal tooth margin. An additional moderately-developed crest extending anteriorly from the apex of the metaloph into the transverse median valley but without a connecting crest from the protoloph. Hindlink well-developed, extending posteriorly and slightly lingually from the metaloph, approximately 5mm lingual to the buccal tooth margin. A thickening in the enamel (the posterior metaconule buttress) posterior to the metaconule apex but probably not developed into a crest. A similar buttress on the posterior flank of the protocone.

DISCUSSION. Palorchestids are rare, fragmentary components of Tertiary fossil assemblages. Until recently, the family consisted of only the primitive, generalised, late Oligocene *Ngapakaldia* and *Pitikantia*, and the derived, highly specialised late Miocene to late Pleistocene *Palorchestes*. The large temporal and morphological gaps separating these groups has made relationships within the family difficult to resolve. Stirton (1967) recognised 4 subfamilies within the Diprotodontidae and included *Ngapakaldia* and *Pitikantia* in the Palorchestinae (later raised to family status) based on similarities in basicranial morphology to *Palorchestes*. However, these supposed apomorphies are also shared with the Diprotodontinae and have since (e.g. Archer 1984) been intepreted as symplesiomorphic within Vombatomorphia. Consequently, Archer (1984) concluded the Palorchestidae was not monophyletic, a view later confirmed by Murray (1986;1990), with his description of *Propalorchestes* dentitions and cranial fragments from the middle Miocene Bullock Creek Local Fauna, Northern Territory, and several Oligo-Miocene sites at Riversleigh. Murray (1990) concluded that *Propalorchestes* is the plesiomorphic sister-taxon of *Palorchestes* and demonsirated a structural transition from the selenodont wynyardiid molar pattern to the bilophodont palorchestid molar pattern. He further concluded that *Ngapakaldia* and *Pitikantia*, having suppressed their selenodont heritage, show closer affinities to the fully bilophodont diprotodontids than palorchestids. Preliminary analyses of late Oligocene and Miocene diprotodontids and palorchestids from Riversleigh further suggest that *Ngapakaldia* and *Pitikantia* should be regarded as primitive members of Diprotodontidae.

Palorchestes anulus supports a *Propalorchestes/Palorchestes* sister-group relationship and confirms doubts (Archer & Bartholomai, 1978; Archer, 1984; Murray, 1990; Mackness, 1995) about the monophyly of the family. The M^1 of *P. anulus* is intermediate in a number of key features between the middle Miocene *Propalorchestes novaculacephalus* from the Bullock Creek Local Fauna, and System C deposits at Riversleigh, and *Palorchestes painei* from the late Miocene Alcoota Local Fauna. The Encore M^1 consistently groups with *Propalorchestes novaculacephalus* and *P. painei* falling within the

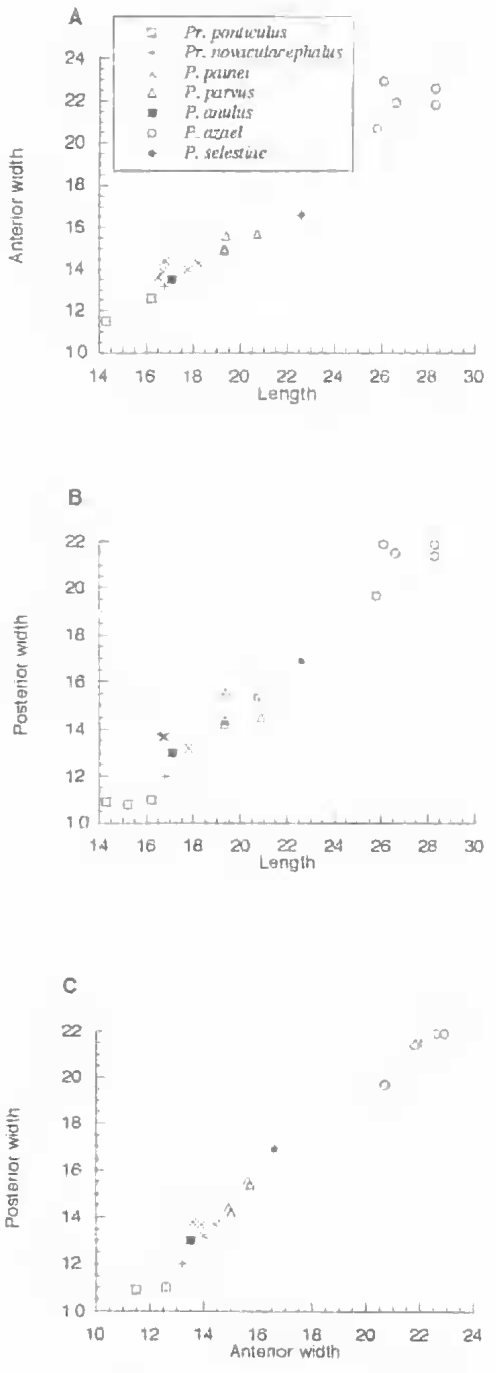

FIG. 2. Bivariate plots of M^1 tooth dimensions for species of *Palorchestes* and *Propalorchestes*: A, length against anterior width; B, length against posterior width; C, anterior width against posterior width. Scale in mm.

size range of both species (Fig. 2A-B). Proportionally (Fig. 2C), however, *P. anulus* groups more closely with *P. painei*. Along the *Propalorchestes-Palorchestes* morphocline (Fig. 2C) there is a noticeable shift towards a squaring-up of the molar crown. *Propalorchestes* molars are more elongate than wide, and trapezoidal in occlusal view, a feature most obvious in the molars of the plesiomorphic *Pr. ponticulus*. In contrast, the posterior width of the M^1 of the highly derived *P. azael*, is similar to its anterior width, giving the tooth a more rectangular profile in occlusal view. The intitial stages of this transition are evident within *P. anulus*. The metaloph of M^1 is less convex than in *Propalorchestes* and approaches the length of the protoloph, thus increasing the posterior width of the molar crown. This feature is reflected in the position of *P. anulus* on the morphocline (Fig. 2C) and is indicative of its derived state relative to *Propalorchestes*.

Other features of the M^1 that indicate *P. anulus* is derived with respect to *Propalorchestes* include its well-developed forelink and accessory forelink and well-developed hindlink; a higher, stronger midlink; a more open transverse median valley; well- developed convex posterobuccal postparaconal and postmetaconal crests; well-developed buttresses on the posterolingual face of the protocone and metaconule; a less convex metaloph; and a well-developed parastyle connected to the protoloph by the forelink. Mackness (1995) listed the well-developed midlink on M^1 as the single synapomorphy of *Palorchestes* as opposed to *Propalorchestes*. The Encore species, with a strong, high midlink, is included in *Palorchestes* as a primitive member of the genus, rather than as a derived species of *Propalorchestes*.

The Encore deposit is regarded to be most probably early late Miocene in age (Archer et al., 1995). Stage-of-evolution biocorrelation of marsupial taxa including vombatids (Krikmann (pers. comm.), propleopine kangaroos (Wroe, 1996), koalas (Archer et al., 1995), dasyurids (Wroe, this volume) and thylacoleonids (Gillespie, this volume) suggest the Encore Local Fauna lies somewhere between Riversleigh's upper System C assemblages and the late Miocene Alcoota Local Fauna and is probably around 10 Ma. The presence of *P. anulus* at Encore Site, structurally intermediate between the middle Miocene *Pr. novaculacephalus* and the late Miocene *P. painei*, further substantiates an early late Miocene age.

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LITERATURE CITED

APLIN, K. & ARCHER, M. 1987. Recent advances in marsupial systematics with a new syncretic classification. Pp. xv-lxxii. In M. Archer (ed.) Possums and opossums: studies in evolution. (Surrey Beatty and Sons and the Royal Zoological Society of New South Wales: Sydney)

ARCHER, M. 1984. The Australian marsupial radiation. Pp. 633- 808. In Archer, M. & Clayton, G. (eds), Vertebrate zoogeography and evolution in Australasia. (Hesperian Press: Perth).

ARCHER, M. & BARTHOLOMAI, A. 1978. Tertiary mammals of Australia: a synoptic review. Alcheringa 2: 1-19.

ARCHER, M., HAND, S.J. & GODTHELP, H. 1995. Tertiary environmental and biotie change in Australia. Pp. 77-90. In Vrba, E.S., Denton, G.H., Partridge, T.C. & Burckle, L.H. (eds), Palaeoclimate and evolution with emphasis on human origins. (Yale University Press: New Haven).

GILLESPIE, A. 1997. *Priscileo roskellyae* sp. nov. (Thylacoleonidae, Marsupialia) from the Oligocene-Miocene of Riversleigh, northwestern Queensland. Memoirs of the Queensland Museum 41: 321-327.

LUCKETT, W. P.1993. An ontogenetic assessment of dental homologies in therian mammals. Pp. 182-204. In Szalay, F.S., Novacek, M.J. & McKenna, M.C. (eds), Mammal phylogeny: Mesozoic differentiation, multituberculates, monotremes, early therians and marsupials. (Springer-Verlag: New York).

MACKNESS, B. 1995. *Palorchestes selestiae*, a new species of palorchestid marsupial from the early Pliocene Bluff Downs Local Fauna, northeastern Queensland. Memoirs of the Queensland Museum 38(2): 603-609.

MURRAY, P. 1986. *Propalorchestes novaculacephalus* gen. et sp. nov., a new palorchestid (Diprotodontoidea: Marsupialia) from the middle Miocene Camfield Beds, Northern Territory, Australia. The Beagle, Occasional Papers of the Northern Territory Museum of Arts and Sciences 3(1): 195-211.

MURRAY, P. 1990. Primitive marsupial tapirs (*Propalorchestes novaculacephalus* Murray and *P. ponticulus* (Marsupialia: Palorchestidae sp. nov.) from the mid-Miocene of north Australia. The Beagle, Records of the Northern Territory Museum of Arts and Sciences 7: 39-51.

RICH, T.H., ARCHER, M. & TEDFORD, R.H. 1978. *Raemeotherium yatkolai* gen. et sp. nov., a primitive diprotodontid from the medial Miocene of South Australia. Memoirs of the National Museum of Victoria 39: 85-91.

STIRTON, R.A. 1967. The Diprotodontidae from the Ngapakaldi Fauna, South Australia. Bureau of Mineral Resources, Geology and Geophysics Bulletin 85: 1-44.

TEDFORD, R.H. & WOODBURNE, M.O. 1987. The Ilariidae, a new family of vombatiform marsupials from Miocene strata of South Australia and an evaluation of the homolgy of molar cusps in the Diprotodontidae. Pp. 401-418. In Archer, M. (ed.). Possums and opossums: studies in evolution. (Surrey Beatty & Sons and the Royal Zoological Society of New South Wales: Sydney).

WROE, S. 1996. An investigation of phylogeny in the giant extinct rat kangaroo *Ekaltadeta* (Propleopinae, Potoroidae, Marsupialia). Journal of Paleontology 70(4): 681-690.

WROE, S. 1997 *Mayigriphus orbus* gen. et sp. nov. a Miocene dasyuromorphian from Riversleigh, northwestern Queensland. Memoirs of the Queensland Museum 41: 439-438.